DEMAND FOR SOCIAL CONTACT IN RATS: TOWARD A QUANTITATIVE ANALYSIS OF SOCIAL REINFORCEMENT VALUE

DEMANDA DE CONTACTO SOCIAL EN RATAS: RUMBO A UN ANÁLISIS QUANTITATIVO DEL VALOR DEL REFORZAMIENTO SOCIAL

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Abstract

Rats were studied in social-release procedures, in which lever presses by one rat released a second rat from a tube restraint for a period of social interaction. Both the fixed-ratio price and the duration of social contact were varied systematically on a within-subject basis, generating a total of 27 demand functions across six subjects. Overall, the data were well accounted for by the essential value model (96% VAF), supporting a social reinforcement view, according to which social-release behavior

is maintained by social contact with another rat. Response rates and parameter fits were comparable in 25-min and 120-min sessions, showing little evidence of satiation. Overall, the findings suggest that socially-reinforced behavior shares functional properties with other reinforcers, and illustrate a promising set of methods for quantifying social reinforcement value.

Key words: social reinforcement, demand analysis, social release, rats

Resumen

Se utilizaron ratas en un procedimiento de liberación social, en el que las presiones a una palanca liberaron a una segunda rata de un tubo de retención durante un período de interacción social. Tanto el valor del programa de razón fija como la duración del contacto social variaron sistemáticamente para cada sujeto, generando un total de 27 funciones de demanda entre los seis sujetos. En general, los datos tuvieron un buen ajuste al modelo de valor esencial (96% VAF), apoyando una visión de reforzamiento social, según la cual el comportamiento de ayuda se mantiene mediante el contacto social con otra rata. Las tasas de respuesta y los ajustes de los parámetros fueron comparados en sesiones de 25 minutos y 120 minutos, mostrando poca evidencia de saciedad. En general, los resultados sugieren que el comportamiento reforzado socialmente comparte propiedades funcionales con otros reforzadores, e ilustra un conjunto prometedor de métodos para cuantificar el valor del refuerzo social.

Palabras clave: reforzamiento social, análisis de demanda, procedimiento de ayuda, ratas

There is ample evidence from both field and laboratory research that social contact can serve as a potent source of reinforcement in a broad range of species, including chimpanzees (Mason, Hollis, & Sharpe, 1962), capuchin monkeys (Dettmer & Fragaszy, 2000), horses (Søndergaard, Jensen, & Nicol, 2011), foxes (Hovland et al., 2011), calves (Holm, Jensen, & Jeppesen, 2002), sows (Kirkden & Pajor, 2006), hamsters (Borland et al., 2017), prairie voles (Beery, Christensen, Lee, & Blandino, 2018), mice (Martin, Sample, Gregg, & Wood, 2014), and rats (Evans et al., 1994; Wilsoncroft, 1968) (see review by Trezza, Campolongo, & Vanderschuren, 2011).

An important role for social contact has recently been shown in social-release procedures, in which animals are provided with opportunities to release a conspecific from some type of restraint. Several recent experiments have shown that rats

will, under a variety of conditions, respond in ways that free a restrained rat (Ben-Ami Bartal, Decety, & Mason, 2011; Ben-Ami Bartal, Rodgers, Sarria, Decety, & Mason, 2014; Hachiga et al., 2018; Hiura, Tan, & Hackenberg, 2018; Sato, Tan, Tate, & Okada, 2015; Schwartz, Silberberg, Casey, Kearns & Slotnick, 2017; Silberberg et al., 2014). In the Ben-Ami Bartal et al. (2011) experiment, two cagemate rats were placed in an arena in which one of the rats (the restrained rat) began the session in a transparent tube-like restraint. The restraint could only be opened from the outside by the unrestrained rat – something a majority of the rats learned to do after about seven 60-min sessions, on average. Once established, the door-opening response continued to occur across sessions, and generally with shorter latencies across the 12 sessions of testing, demonstrating a learning effect. Furthermore, the proportion of rats that opened the restraint was significantly higher in conditions with a restrained rat, compared to conditions with an empty restraint and a restraint with an inanimate toy rat, showing that release depended at least in part on the presence of the restrained rat.

Although Ben-Ami Bartal et al. (2011) favored an empathy-based interpretation, in which door-opening is motivated by relieving the distress of the restrained rat, the behavior is equally compatible with an operant-learning interpretation, in which door-opening is an operant, occurring under discriminative control of a restrained rat, and maintained by contingent social release of that rat. And, as discussed previously, social contact can itself function as a reinforcer. The role of social reinforcement alone in social release was called into question, however, in one phase of the Ben-Ami Bartal et al. (2011) experiment, in which door opening released the restrained rat into an adjacent chamber that did not permit direct social contact. Door-opening was maintained under these conditions, but only in rats for which social release had been well established after 12 sessions of training. In a replication and follow-up study, Silberberg et al. (2014) showed that a history of contingent social contact between the unrestrained and restrained rats was necessary to produce door opening for nonsocial contact; absent such a history, social release into an adjacent chamber could not be established. More recent experiments have confirmed this strong role of social reinforcement (and stimuli correlated with social reinforcement) in a related paradigm (Hachiga et al., 2018; Hiura et al., 2018; Schwartz et al., 2017).

Hiura et al. (2018), for example, assessed the value of social and food reinforcers under a range of schedules and motivational conditions. Progressive-ratio (PR) schedules were used, in which the response requirements increased systematically

with each reinforcer delivered (a food pellet or 10-s social contact). Responding was maintained by both reinforcers, though response rates were higher for food than for social reinforcers. This was true both in single schedule (Experiment 1) and concurrent schedule (Experiment 2) arrangements. Social responding decreased to low levels in extinction conditions, when it was no longer effective in opening the door for social access, showing that social contact did indeed serve operant functions. Responding was maintained at moderate levels by stimulus changes (tone, door opening) even in the absence of a restrained rat, showing an enduring effect of conditioned reinforcement via stimuli previously coupled with social release.

The available evidence to date from social-release procedures is consistent with the proposition that social contact (and correlated stimuli) can serve as potent reinforcing events (Hachiga et al., 2018; Hiura et al., 2018; Schwartz et al., 2017; Silberberg et al. 2014). Little is known, however, about even the most basic functions of social contact as a reinforcer in these procedures. The main objective of the present experiment was to replicate and extend prior research using social contact as a reinforcer with rats in social-release procedures, but across a wider parametric range of conditions that permit sharper quantitative analyses of basic social reinforcement functions, essential to a comprehensive analysis of social reinforcement.

Of particular interest were the functions relating the value of social contact to its magnitude (duration of social contact) and to its costs (number of responses to produce it). Social reinforcement magnitude was systematically manipulated via changes in the duration of social access (10 s, 30 s, and 60 s). Although reinforcement magnitude has long been considered a fundamental dimension of reinforcement, its effects are a complex function of many interacting variables (Bonem & Crossman, 1988). With food reinforcers, some experiments report a positive relation between responding and food amount (Bradshaw, Szabadi, & Bevan, 1978), some an inverse relation (Harzem, Lowe, & Priddle-Higson, 1978), and some both increases and decreases in the same study (Reed, 1991). With less conventional reinforcers, such as wheel running, there is an inverse relation between responding and duration of access (Belke, 1997). Even less is known about how social reinforcers are affected by the duration of their access. Detailed parametric data on reinforcer duration effects are therefore important in mapping out basic social reinforcement functions.

The costs of social contact were effort-based, arranged as fixed-ratio (FR) schedules altered systematically across conditions. These generated demand functions, defined in terms of obtained social reinforcers as a function of FR price, for each of the three reinforcer duration conditions (10 s, 30 s, 60 s of social contact), permit-

ting direct quantitative comparisons of reinforcer magnitude effects. The data were analyzed using Hursh and Silberberg's (2008) essential value model:

$$\log Q = \log Q_0 + k(e^{-\alpha P} - 1),$$

where demand (Q) is consumption rate (number of social reinforcers per unit time) as a function of unit price (P, FR requirement); Q_0 is the consumption at the lowest price. The slope of the function (α) expresses elasticity, or sensitivity to price changes. Two additional parameters are P_{max}, the maximum price before the function turns from inelastic to elastic (slope = −1.0), and O_{max}, the peak response output. Among the chief advantages of this model is that it provides a common metric for assessing reinforcer efficacy – the essential value ($1/\alpha$) of different reinforcers.

The model has proven successful in assessing the value of a variety of reinforcers and species (Barrett & Bevins, 2012; Bentzley, Fender, & Aston-Jones, 2013; Cassidy & Dallery, 2012; Christensen, Silberberg, Hursh, Huntsberry, & Riley, 2008; Fragale, Beck, & Pang, 2017; Rasmussen, Robinson, & Rodriguez, 2016), but has yet to be applied to the reinforcing value of social contact. In the present study, demand for social reinforcement was systematically explored at three different reinforcer durations, and analyzed in relation to the essential value model. These methods permitted a more precise quantitative analysis of the value of social contact as a reinforcer, and contribute to a growing body of research on basic mechanisms of social reinforcement and social learning. Successful application of this model to the present findings would provide further evidence of social reinforcement mechanisms in the social-release paradigm.

Methods

Subjects

Six pairs of Long Evans rats served as subjects. All rats were pair-housed throughout the experiment. Two of the pairs were females (designated BB and PP), approximately four months of age at the start of the experiment; two of the pairs were males (M1, M3), approximately four months of age; and the other two pairs of rats were males (BYR, BRR), approximately 12 months of age. One rat in each pair was randomly assigned as the "focal" rat (the one with access to the lever) and the other the "restrained" rat (the one in the restraint tube). One female focal rat (cagemate
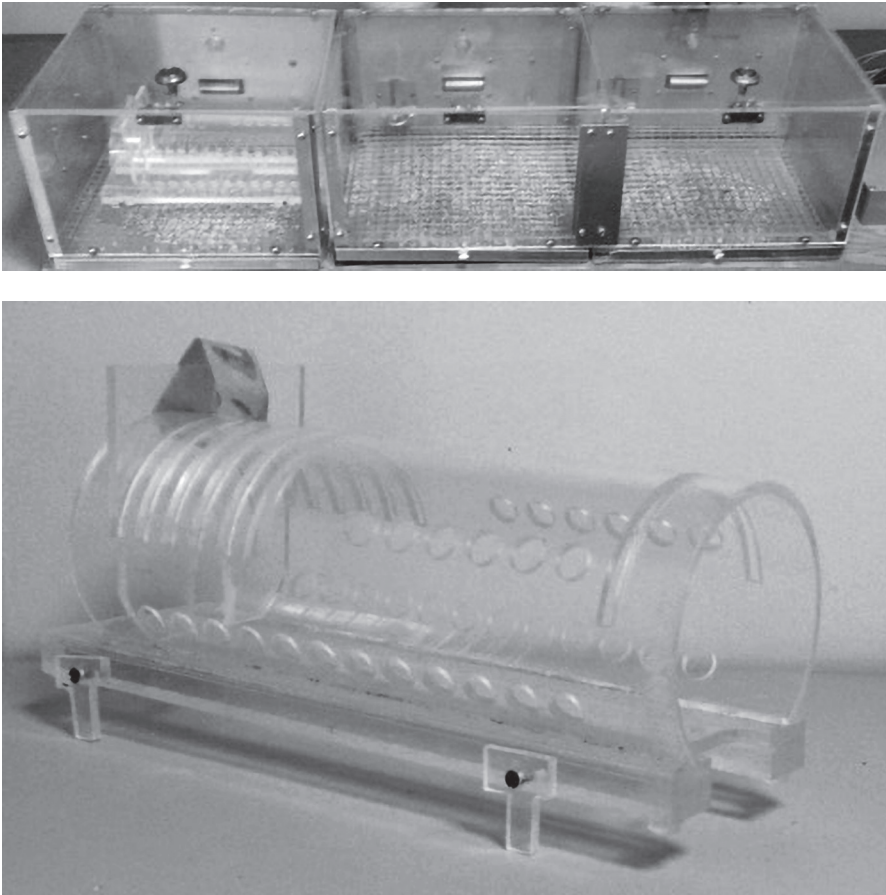
Figure 1. Rate of inappropriate mealtime behavior per minute across attention, escape, no interaction, and control conditions during functional analysis sessions.

of PP) died during the experiment, between the two main phases, and was replaced with a rat of the same age and sex for the remainder of the experiment. Housing was provided in a temperature- and humidity-controlled environment, with a 12-hr light/dark cycle. Home-cage access to food chow (Lab Diet 5012, Brentwood, MO) was restricted for 20-22 hours prior to each session.

Apparatus

The apparatus consisted of three conjoined experimental chambers (see Figure 1). The center and right chambers were open to each other, but separated from the left

chamber by a Plexiglas barrier. A 5.5 cm diameter hole, 1.5 cm above the floor, was cut into the barrier wall, but the hole was blocked by a metal door hinged at the back of the chamber and opened upwards at a 90-degree angle. The leftmost chamber contained a Plexiglas rodent restraint tube (Harvard Apparatus®, Holliston, MA), 8 cm diameter x 24.5 cm length, access to which was separated by the mechanical metal door that opened into the center chamber. The left side of the tube had an adjustable-length barrier, permitting maximum mobility for the rat inside the restraint, and 18 air holes on each side of the tube provided ventilation. The center and right chambers contained response levers (5 cm x 1.5 cm x 1.5 cm), mounted 6 cm above the floor and 4.5 cm below a stimulus lamp (which could be illuminated with white light), but only the lever in the right chamber was active during the experiment. The center chamber also contained a food cup, into which 45 mg sucrose banana flavored pellets (BioServ Dustless Precision Pellets®) could be dispensed. Experimental events were controlled by a Macintosh® computer, running Microsoft Visual Studio 2008® in a parallel operating system (Windows 7®).

Preliminary training

Restrained rat training. Following 1-2 sessions of adaptation to the apparatus, restrained rats underwent a series of conditions designed to train exit from the restraint. In this stage of training, the door was opened via the experimenter controlling the computer program (accompanied by 1 kHz tone of 1 s duration) until the rat left the tube, at which point the door was closed and the rat was returned to the tube. When reliable exiting was observed, the delay between successive openings was increased according to variable-time (VT) schedules until an average delay of 30-s was achieved. All phases of preliminary training required a total of 18 sessions, on average, to establish reliable restraint exiting (range 14-21 sessions across rats).

Focal rat training. Four of the six focal rats (BB, PP, M1, M3) were trained to press the lever in the right chamber via the differential reinforcement of successive approximations with contingent food delivery in the center chamber. When lever pressing had been established and was maintained at a consistent rate (requiring an average of 7.5 25-min sessions), social contact was substituted for food delivery. At this point, the experiment proper began, and the food was not used again in the experiment. Two pair of rats (BYR, BRR) had acquired lever pressing for food in a prior experiment and did not require this preliminary training.

Experimental procedures

Only the lever in the rightmost chamber was used to open the door to the restrained rat, and a light above the lever signaled when lever presses by the focal rat would open the door and activate the tone. The door was then closed when the focal and restrained rats were in social contact; this started the reinforcer period. In most cases, this was when the restrained rat emerged from the restraint, and the social interaction period occurred in the center and right chambers. The four younger focal rats (BB, PP, M1, M3) were small enough to fit in the tube with the restrained rat and occasionally entered the tube prior to the restrained rat exiting. When this happened, the door was closed, and the social interaction period occurred in the tube. In either case, when the reinforcer period ended, a signal on the computer monitor alerted the experimenter to replace the restrained rat to the tube, and the focal rat to the lever-pressing chamber. The next trial then began, signaled by the light above the right lever. Only responses that occurred in the presence of this light counted toward the schedule requirement; responses during the reinforcer period were counted toward the total responses but removed from the analysis (as these could have been made by the other rat).

FR demand functions for social contact were generated on a within-subject basis for each of the six rats. This was accomplished by means of systematic increases in FR requirements across reinforcement magnitude conditions. Each FR series within a social reinforcement magnitude (prespecified duration of social contact) began at FR 1 (a single lever press activated the door-opening and the tone) and increased across sessions according to the following geometric progression: 1, 2, 5, 10, 20, 40, 80, 160. The progression continued until a price was reached at which no reinforcers were earned in a session, whereupon the next sequence began at FR 1. The number of FR schedules in the series therefore depended on when responding declined to low levels, but in all cases the functions had at least 4 (and up to 7) FR values.

Table 1 shows the sequence of conditions and the number of sessions in each condition per rat. The FR 1 condition in each series served as a baseline, and remained in place until response rates did not vary more than 20% across three consecutive sessions; this required approximately 10 sessions. In most nonbaseline conditions, the FR prices were in effect for a single session, but due to equipment malfunction or human error, additional sessions occasionally occurred. In some early conditions for BYR and BRR, additional sessions were conducted deliberately at the highest price on the demand function. Demand functions were conducted at each of three different durations of social contact: 10 s, 30 s, and 60 s, in that order.

Table 1. Number of sessions per rat in Phase 1 conditions.

Condition	BB	PP	M1	M3	BYR	BRR
10 s						
FR 1	10	10	24	16	10	10
FR 2	1	1	2	1	1	1
FR 5	1	1	1	1	1	1
FR 10	1	1	1	1	5	5
FR 20	1	1	1	1	-	-
FR 40	2	1	-	-	-	-
FR 80	-	1	-	-	-	-
30 s						
FR 1	9	11	6	11	10	10
FR 2	1	1	1	1	1	1
FR 5	1	1	1	2	1	1
FR 10	1	1	1	1	1	1
FR 20	1	1	1	1	1	1
FR 40	2	1	-	1	10	10
60 s						
FR 1	10	9	14	7	8	16
FR 2	2	1	1	1	2	1
FR 5	1	1	1	1	1	1
FR 10	1	1	1	1	1	1
FR 20	1	1	1	1	1	5
FR 40	1	1	-	-	6	-
10 s						
FR 1	12	18	-	-	11	-
FR 2	2	1	-	-	1	-
FR 5	1	1	-	-	1	-
FR 10	1	1	-	-	1	-
FR 20	1	1	-	-	1	-
FR 40	1	-	-	-	1	-

To assess potential order effects, the 10-s duration condition was replicated after the 60-s duration condition for three of the six rats (BB, PP, BYR).

The experiment was divided into two phases, defined by session duration: 25 min in Phase 1 and 120 min in Phase 2. The 120-min sessions were conducted to bring the procedures into somewhat closer alignment with extended sessions more commonly used in experiments with demand functions, in which a greater proportion of daily access to reinforcement occurs within the session. Table 2 shows the sequence of conditions and the number of sessions in each condition per rat in Phase 2. Four rats (BB, PP, M1, M3) started Phase 2 conditions, but for only two of them (BB, PP) was responding sustained (see below). For these two rats, three additional demand functions (one at each reinforcer duration across the geometric FR progression) were generated for the 120-min (Phase 2) sessions. By this time, the rats had extensive exposure to baseline (FR 1) schedules, so responding was quicker to stabilize; these conditions were therefore run for three sessions to establish a baseline, rather than approximately 10 sessions with the 25-min (Phase 1) sessions. The same condition-termination criteria were in place (no reinforcers earned in a session) before adjusting the social reinforcement duration, but because responding was sustained at higher FR prices (up to FR 160) for Phase 2 sessions, these functions consisted of 7-8 FR values.

Results

Appendix A shows response rates and obtained reinforcer rates per session under all conditions for each rat. Figure 2 shows normalized demand functions, separately for the different reinforcer durations (10 s, 30 s, 60 s), for the 25-min (Phase 1) sessions for all six focal rats. In conditions with greater than three baseline sessions (see Table 1), only data from the final three sessions were used in the analysis. In conditions with more than one nonbaseline session, only data from the first session was used in the analysis. In all, 394 sessions were used in the analysis.

Quantitative fits of the demand functions were performed using Hursh and Silberberg's (2008) model, with Q_0 and α free to vary, and k set as a constant, calculated for each individual subject as (maximum log consumption – minimum log consumption) + 0.5. Given the variable response outputs and active session durations, response outputs were calculated as an hourly rate. All data were used for the demand curve fits, excluding sessions where consumption equaled 0 (see Appendix A).

For FR values that were replicated over multiple days, mean consumption was used for model fits.

The model provided a good description of the data overall, accounting for an average of 96% of total variance (range = 78%-98% across rats), and between 92%-99% across the three reinforcer durations (range = 70%-99% across rats). Normalized reinforcer magnitude units (q) were calculated using the equation q =100/B, where B is consumption at the lowest price (FR 1). Consumption at each FR value was multiplied by q to obtain normalized consumption; normalized price was calculated as FR/q. The four main parameters of the model (elasticity, consumption at lowest price, maximum response output, and price at which maximum consumption occurred) are plotted in Figure 3 for all six focal rats at all three reinforcer durations.

Despite the good overall fits, there were some between-subject differences in the basic parameters. For five of six rats (all except BYR), the obtained rate of social reinforcement at the lowest price, Q_0, was higher at the shortest reinforcer duration (10 s) than at the longest (60 s) duration (Figure 3, upper left panel). In other words, more 10-s social reinforcers were produced than 60-s reinforcers, even when computed as rates to account for differences in response opportunities. Similarly, for four of these five rats, $1/\alpha$ (Figure 3, lower left panel) was higher in the 10-s reinforcer duration than in the longer reinforcer durations, indicating higher essential value (less elastic demand). While the other two rats

Table 2. Number sessions per rat in Phase 2 conditions.

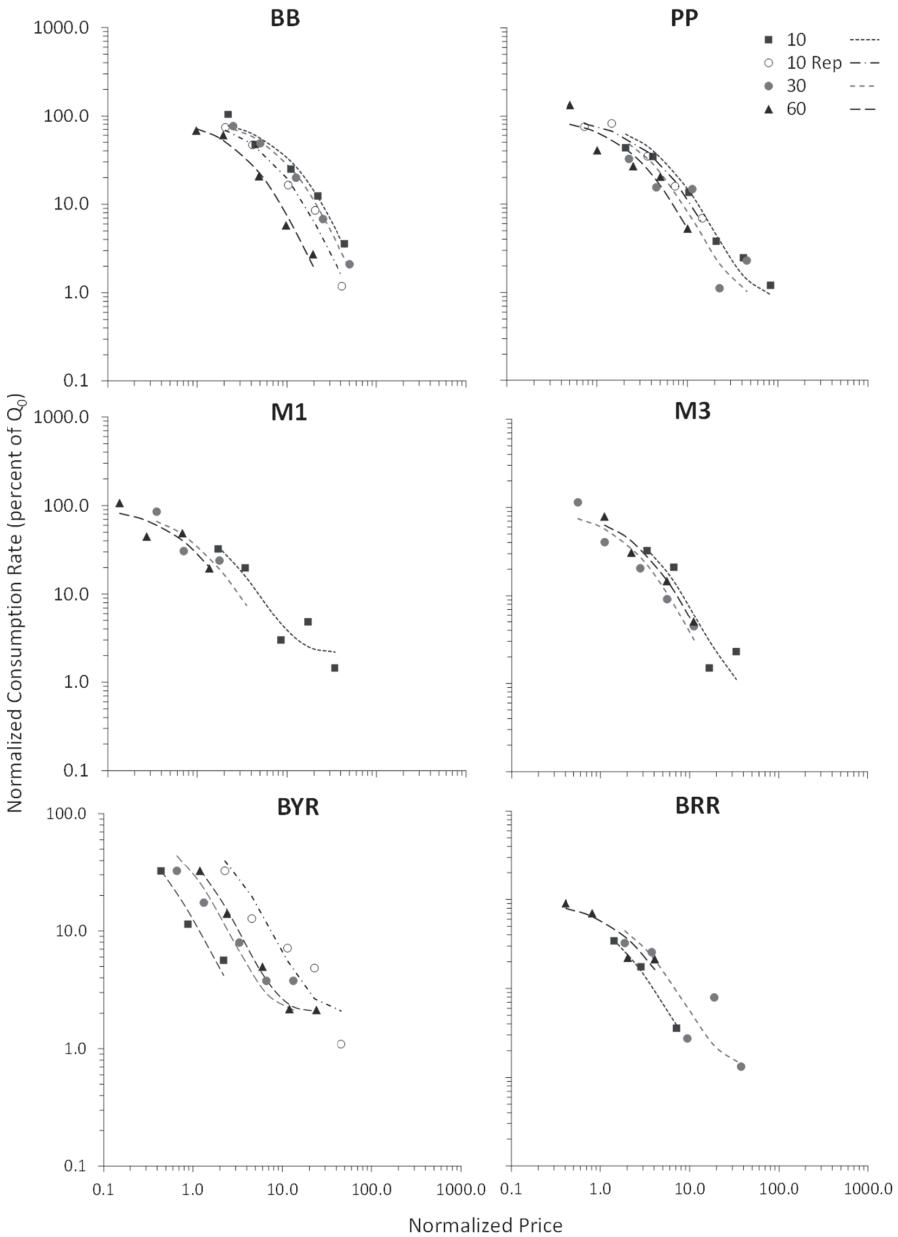| Condition	BB	PP
10 s		
FR 1	3	3
FR 2	1	1
FR 5	1	1
FR 10	1	1
FR 20	1	1
FR 40	1	1
FR 80	1	1
FR 160	1	1
30 s		
FR 1	3	3
FR 2	1	1
FR 5	1	1
FR 10	1	2
FR 20	1	1
FR 40	1	1
FR 80	1	1
FR 160	1	-
60 s		
FR 1	3	3
FR 2	1	1
FR 5	1	1
FR 10	1	1
FR 20	1	1
FR 40	1	1
FR 80	1	1
FR 160	1	1

Figure 2. Normalized consumption as a function of normalized FR price under all 3 reinforcer durations in Phase 1 (25-min sessions).
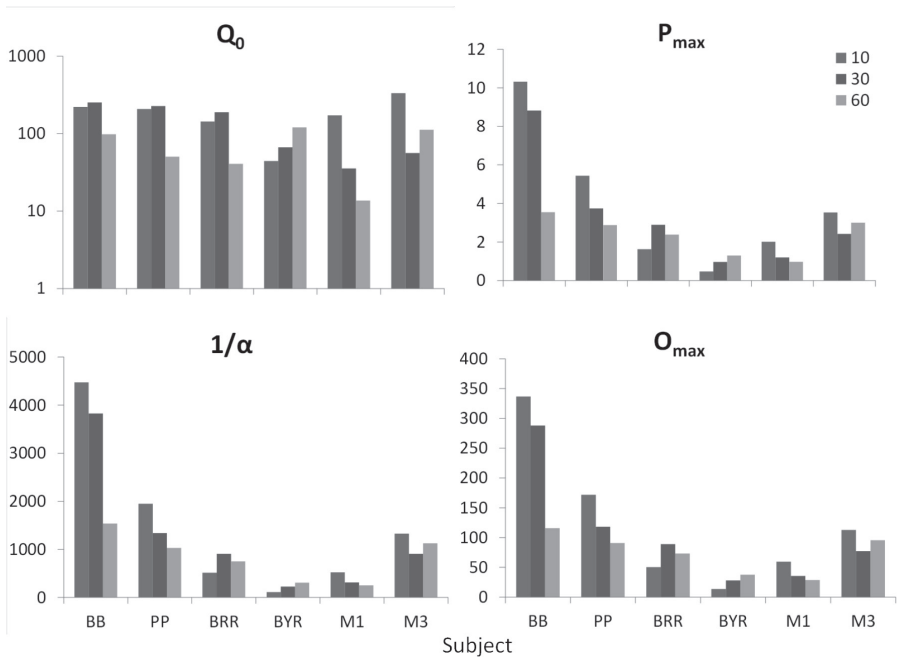
Figure 3. Four basic parameters of the model for each reinforcer duration in Phase 1 (25-min sessions).

(BRR, BYR) showed a different profile, with higher essential value associated with the longest than the shortest reinforcer duration, the differences were small, and reversed in the replication, with the 10-s reinforcer showing the highest essential value (see BYR, Figure 2), in line with four of the other rats (BB, PP, M1, M3).

Figure 4 shows the demand functions for the Phase 2 sessions for the two female rats (BB and PP), for whom responding could be sustained. Rats M1 and M3, the two male rats of the same age as the females, were also studied in Phase 2, but responding was not consistently maintained under baseline conditions. These conditions were therefore discontinued for these two rats. For BB and PP, however, responding was well maintained in the Phase 2 sessions, with the functions roughly comparable to those from the Phase 1 sessions (see Figure 2). Effects of reinforcer duration were less pronounced in Phase 2 sessions than in Phase 1 sessions, especially for Rat BB, with overlapping demand functions (Figure 4). Similar to the Phase 1 sessions, the essential value model provided a good overall description of the data (96 %VAF).
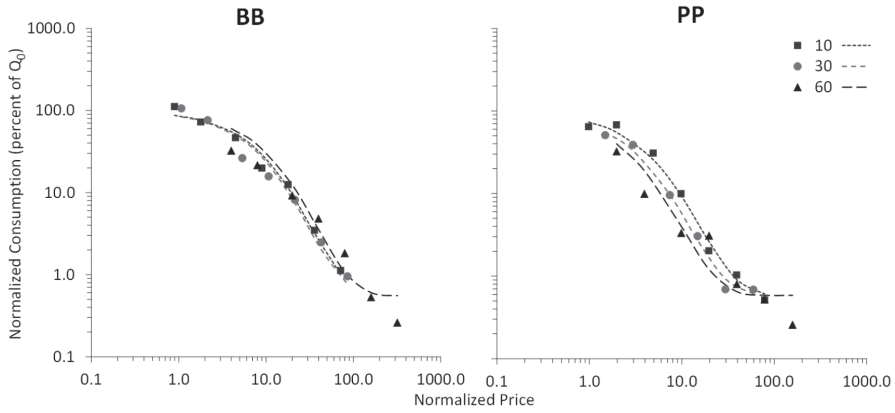
Figure 4. Normalized consumption as a function of normalized FR price under all 3 reinforcer durations for female rats in Phase 2 (120-min sessions).
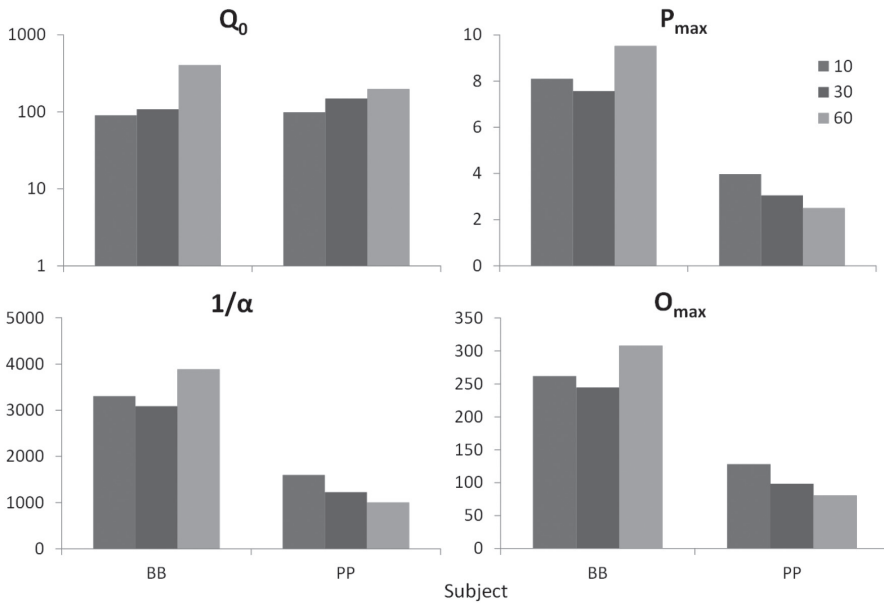

Figure 5. Four parameters from the model for each reinforcer duration for female rats in Phase 2 (120-min) sessions.

The four main parameters of the model for Phase 2 conditions are plotted in Figure 5. Relative to the 25-min (Phase 1) sessions, three of the parameters ($1/\alpha$, P_{max}, and O_{max}) were not as sensitive to reinforcer duration. The functions were shallower and less systematically related to reinforcer duration than in the Phase 1 sessions. This is consistent with the converging reinforcer-duration functions in Phase 2 sessions. The one parameter that did vary systematically with reinforcer duration was Q_0 (consumption at the lowest price), such that relative consumption increased directly with reinforcer duration, indicating higher relative reinforcer value with longer social access.

Despite the longer sessions in Phase 2, overall response rates were comparable to those seen in the shorter Phase 1 sessions for these two rats (see Appendix A). Because responding was maintained at higher prices in Phase 2 sessions, these functions also included a wider range of FR prices. Even at these higher prices, however, response rates were roughly comparable to those seen at lower prices in the Phase 1 sessions. Mean response rates across the range of prices from FR 1-20 were 2.89 per min (Phase 1) versus 2.73 per min (Phase 2) for Rat BB, and 1.64 per min (Phase 1) versus 1.21 for Rat PP.

A within-session analysis is provided in Figures 6 and 7, which shows cumulative response curves under the 10-s reinforcer duration for Phase 1 (replication) (top panels) and Phase 2 (bottom panels) conditions for the two female rats BB and PP (Figures 6 and 7, respectively). The vertical reference line in the 120-min Phase 2 plots indicates the end of the 25-min mark of the shorter Phase 1 sessions. Despite differences in scale, within-session response rates for each rat were generally comparable in Phase 2 and Phase 1 sessions. The price at which peak responding occurred differed, however, for Phase 1 and Phase 2 sessions. For Rat BB, peak responding occurred at FR 10 in Phase 1 and FR 20 in Phase 2; for Rat PP, peak responding occurred at FR 20 in Phase 1 and FR 5 in Phase 2. In the Phase 2 conditions, peak responding yielded social contact times of 200 s and 350 s for Rats BB PP, respectively.

Discussion

Responding in all six rats was maintained across a wide range of social reinforcement conditions, in which lever presses provided contingent access to another rat. The results join with those of prior research and are broadly consistent

Figure 6. Representative cumulative response curves at each FR price for 10-s social access for Rat BB in Phase 1 (25-min sessions, replication condition) (top) and Phase 2 (120-min sessions) (bottom). The reported FR 1 session was the session immediately preceding the FR 2 session. The vertical reference line in the 120-min Phase 2 plot indicates the end of the 25-min mark of the shorter Phase 1 sessions. Note that the y-axes are scaled individually to accommodate different overall response rates.

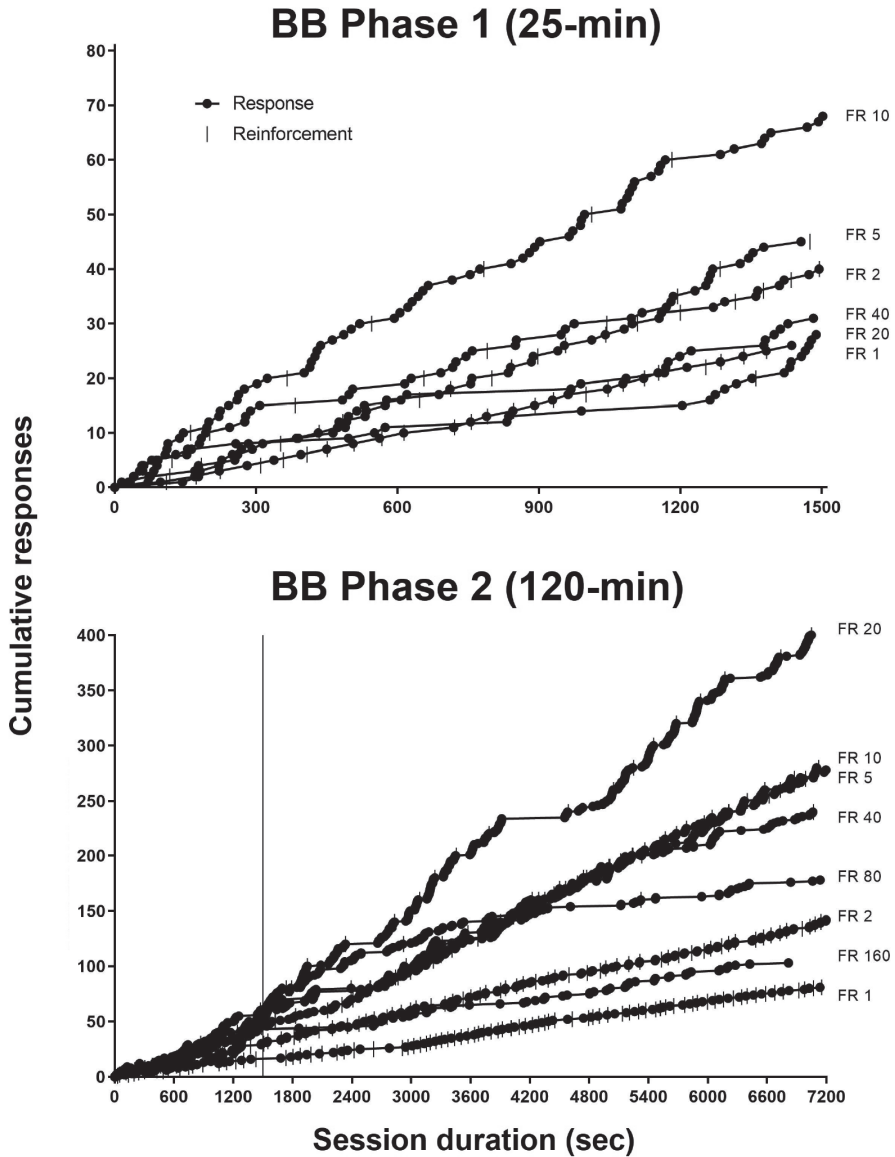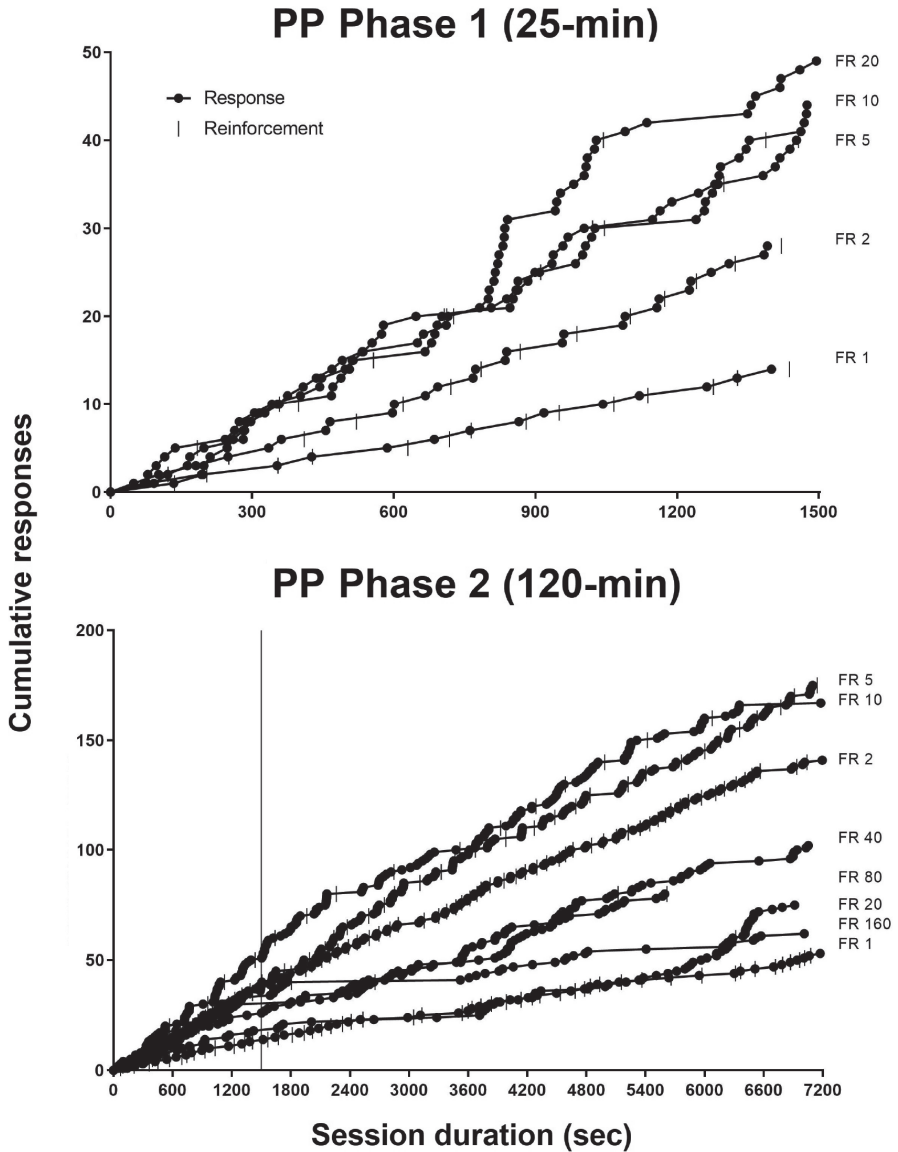# PP Phase 1 (25-min)

PP Phase 2 (120-min)

Figure 7. Representative cumulative response curves at each FR price for 10-s social access for Rat PP in Phase 1 (25-min sessions, replication condition) (top) and Phase 2 (120-min sessions) (bottom). See Figure 6 for other details.

with the social reinforcement hypothesis – the view that behavior in the social-release paradigm is driven largely by contingent access to social stimuli (Hiura et al., 2018). Although not all previous experiments have been interpreted in such terms (e.g., Ben-Ami Bartal et al., 2011, 2014; Sato et al., 2015), the pattern of results from these experiments can all be viewed as operant behavior reinforced by social access (Schwartz et al., 2017; Silberberg et al., 2014). The main aim of the present experiment was to replicate and extend these prior findings across a wider range of experimental conditions and in more quantitatively precise terms, using demand methods for analyzing reinforcer value. On the whole, the demand functions were well described by Hursh and Silberberg's (2008) essential value model (96% VAF). The overall fits are comparable to those seen with other reinforcers (Barrett & Bevins, 2012; Bentzley et al., 2013; Cassidy & Dallery, 2012; Christensen, et al., 2008; Fragale et al., 2017; Rasmussen et al., 2016), suggesting that social contact shares functional characteristics with a wide array of other reinforcers analyzed in similar terms.

The effects of reinforcement duration were less clearcut than the effects of price. In the Phase 1 (25-min) sessions, 10-s access to the other rat was of higher value than the 60-s access times in a majority of cases, as reflected in higher essential value $(1/\alpha)$ (less sensitive to changes in price), higher Q_0, higher P_{max} and higher O_{max} values. There was less sensitivity to duration of social contact in Phase 2 (120-min) sessions, however, suggesting perhaps that differences in duration of social contact may matter less with greater overall access time. These conditions (Phase 2) were conducted with only two rats, however, so firm conclusions await additional research examining in further quantitative detail the effects of duration of social access on reinforcer value.

Such future research might also use procedures better suited to detect reinforcer duration effects. While the literature on reinforcer duration effects is, on the whole, somewhat mixed and difficult to interpret (Bonem & Crossman, 1988), some procedures nonetheless have proven more sensitive to reinforcer duration effects than others, including (a) response-contingent magnitude changes, (b) within-session variation in magnitude, (c) differentially signaled magnitudes, and (d) concurrent rather than single schedules. Because none of these procedural features were present in our procedures, it is possible that the reasons for the present mixed results lies with the procedures, and that more sensitive methods may have revealed stronger sensitivity to social reinforcer duration. This should be a key priority for future research.

There was no evidence the restraint acquired aversive functions, as required by empathy-based accounts (Ben-Ami Bartal et al., 2011; Sato et al., 2015), according to which the focal rat is motivated to relieve distress on the part of the partner rat. Not only was behavioral evidence of distress in either rat absent, there were contrary observations that access to the tube served reinforcing functions. The rats not only entered the tube, but the smaller rats in some cases did this simultaneously (i.e., spent time together inside the tube). Similar observations have been reported in prior research (Ben-Ami Bartal et al., 2011; Hiura et al., 2018), and are plainly difficult to reconcile with the aversiveness of the restraint. It might be argued, however, that the present procedures acted to dampen aversive functions for the restrained rats, thereby generating less distress (conditioned emotional responses). The pretraining our restrained rats received was carried out to bring leaving the restraint under discriminative control of the open door and tone, thereby minimizing delays to social contact. Prolonged exposure to the restraint in these training sessions (18 sessions, on average), however, may have attenuated or extinguished any early conditioned responses on the part of the restrained rat, had they been present. Thus, while we cannot completely rule out restraint-induced distress for the entirety of the experiment, such distress would have played little if any role in steady-state conditions that were the focus of the present experiment. Further, if the restrained rat is not in distress, it cannot serve as empathic motivation for the focal rat.

By its nature, social interaction depends on the behavior of another; the value of social interaction as a reinforcer therefore is a complex function of many interacting variables, including not only the quantity (duration) of social interaction, but its quality as well – the types of behavior it enables (e.g., play, grooming). Although we did not analyze behavior within the social contact episodes, the rats were consistently engaged socially with one another, consistent with social reinforcement functions. It may be relevant that the rats were very familiar with one another. As with most prior research in this domain, the focal and restrained rats in the present experiment were cagemates (i.e., they lived together in the same cage outside the experiment). There are reports in the literature in which access to an otherwise unfamiliar (novel) rat has supported release behavior (Ben-Ami Bartal et al., 2014), but little is known about the generality of these effects – the range of conditions under which familiarity contributes to social reinforcement value. This is an important direction for future research, and one for which quantitative methods are ideally suited. Assessing demand and preference for familiar versus unfamiliar rats would shed important light on the contributions of social familiarity and novelty to social reinforcer value.

Future research should also explore more systematically sex differences in sociality. Response rates for the four male rats were comparable to those reported by Hiura et al. (2018) with male rats on similar procedures. Response rates for the two female rats were consistently higher than the males, however, even in the Phase 2 sessions (see Appendix A). Indeed, these were the only rats for which functions were obtainable at the longer (Phase 2) session lengths (Figure 4), where these female rats responded consistently throughout the sessions (Figures 6 and 7). These robust levels of responding may reflect relatively higher social responsiveness for female than for male rats, although small sample sizes preclude more meaningful comparisons. Most prior research has used male rats only, though Ben-Ami Bartal et al. (2011) found a higher percentage of female rats learned to open the door (6/6), compared to male rats (17/24). As with the present study, however, small sample sizes made more direct comparisons difficult. Future research would be wise to examine more systematically sex differences in the value of social reinforcers. The present procedures would lend quantitative precision to such comparisons.

Social-release procedures are also well suited to cross-species comparisons. Although to date most of the research has been conducted with rats, one can easily imagine the procedures adapted to other species, allowing, of course, for differences in the way that social release may operate for different species in different ecological conditions. On the other hand, if one is primarily interested in the social reinforcement functions of social-release procedures, it may be worthwhile to bypass the restraint entirely (i.e., arrange for access to an unrestrained social partner). Doing so would simplify the method while also improving ecological validity of the social interaction. It would also facilitate contact with the broader literature on social reinforcement. Of the three most common laboratory-based procedures for studying social reinforcement identified in the Trezza et al. (2011) review—conditioned place preference, maze learning, and operant procedures—the latter are on the rise, increasingly favored for their quantitative rigor.

Borland et al. (2017), for example, made 20-s periods of social contact contingent on an operant response (door entry) in hamsters, and manipulated the costs of social interaction with a free-ranging partner by increasing the weights on the door across consecutive sessions. The number of entries declined systematically as a function of door weight, in much the same way as lever pressing declined with FR price in the present experiment. Demand for social contact thus appears to be affected in similar ways in the two procedures, whether costs are measured as weight or as response requirements, and apparently irrespective of whether social contact

is preceded or not by release from a restraint. In the context of assessing social reinforcement functions, then, the restraint may be unnecessary. Future research would profit from broadening the methods for arranging social interaction as a reinforcer, including but not limited to social-release procedures.

In sum, the present findings contribute to an expanding body of research on socially-reinforced behavior, adding quantitative precision to the definition of social reinforcement value. That demand for social contact was affected by its costs in much the same way as for other reinforcers suggests functional parallels. At the same time, some effects of other variables (e.g., duration of social contact, session duration) were less clearcut and warrant additional research. Perhaps most useful at this early stage of the analysis of social reinforcement are parametric data sets exploring a wide range of variables with well-known effects on other reinforcers— amount, immediacy, rate, probability, quality, novelty, to name a few. This would facilitate comparisons to other reinforcers analyzed in similar terms, including both what social reinforcers share with other reinforcers as well as some of their unique characteristics.

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Appendix A

Rat	Phase	Social reinforcement duration (s)	FR schedule	Mean (SD) responses per min	Mean (SD) reinforcers per min
BB	1	10	FR 1	3.83 (0.47)	3.83 (0.47)
		10	FR 2	3.66	1.74
		10	FR 5	4.60	0.92
		10	FR 10	4.63	0.46
		10	FR 20	2.73	0.13
		10	FR 40	1.28	0.00
		30	FR 1	3.32 (0.56)	3.19 (0.66)
		30	FR 2	4.36	2.05
		30	FR 5	4.65	0.84
		30	FR 10	3.38	0.29
		30	FR 20	2.51	0.09
		30	FR 40	1.00	0.00
		60	FR 1	1.14 (0.72)	1.10 (0.74)
		60	FR 2	1.96	0.98
		60	FR 5	1.82	0.34
		60	FR 10	0.94	0.09
		60	FR 20	1.19	0.04
		60	FR 40	1.56	0.00
		10	FR 1	2.57 (0.09)	2.53 (0.15)
		10	FR 2	3.28 (0.24)	1.60 (0.17)
		10	FR 5	2.82	0.56
		10	FR 10	3.31	0.29
		10	FR 20	1.14	0.04
		10	FR 40	1.24	0.00
PP	1	10	FR 1	1.56 (0.16)	1.50 (0.17)
		10	FR 2	2.55	1.20
		10	FR 5	2.62	0.47
		10	FR 10	1.31	0.13

		10	FR 20	1.88	0.09
		10	FR 40	1.66	0.04
		10	FR 80	0.96	0.00
		30	FR 1	1.22 (0.91)	1.22 (0.91)
		30	FR 2	1.30	0.58
		30	FR 5	2.79	0.56
		30	FR 10	0.59	0.04
		30	FR 20	1.73	0.09
		30	FR 40	0.72	0.00
		60	FR 1	1.12 (0.17)	1.12 (0.17)
		60	FR 2	0.68	0.34
		60	FR 5	1.12	0.22
		60	FR 10	1.71	0.17
		60	FR 20	1.28	0.04
		60	FR 40	1.36	0.00
		10	FR 1	0.93 (0.45)	0.91 (0.41)
		10	FR 2	1.99	1.00
		10	FR 5	2.11	0.42
		10	FR 10	2.13	0.19
		10	FR 20	2.06	0.08
BYR	1	10	FR 1	0.24 (0.12)	0.24 (0.12)
		10	FR 2	0.17	0.08
		10	FR 5	0.25	0.04
		10	FR 10	0.04	0.00
		30	FR 1	0.36 (0.29)	0.36 (0.29)
		30	FR 2	0.43	0.19
		30	FR 5	0.44	0.09
		30	FR 10	0.54	0.04
		30	FR 20	0.92	0.04
		30	FR 40	0.48	0.00
		60	FR 1	0.65 (0.17)	0.65 (0.17)

		60	FR 2	0.56 (0)	0.28 (0)
		60	FR 5	0.69	0.10
		60	FR 10	0.69	0.04
		60	FR 20	0.85	0.04
		60	FR 40	0.48	0.00
		10	FR 1	1.23 (0.12)	1.23 (0.12)
		10	FR 2	1.10	0.48
		10	FR 5	1.36	0.27
		10	FR 10	1.84	0.18
		10	FR 20	0.96	0.04
		10	FR 40	0.72	0.00
BRR	1	10	FR 1	0.81 (0.38)	0.81 (0.38)
		10	FR 2	0.83	0.42
		10	FR 5	0.59	0.08
		10	FR 10	0.20	0.00
		30	FR 1	1.02 (0.43)	1.02 (0.43)
		30	FR 2	1.68	0.80
		30	FR 5	0.56	0.09
		30	FR 10	2.49	0.25
		30	FR 20	1.50	0.04
		30	FR 40	0.60	0.00
		60	FR 1	0.61 (0.15)	0.61 (0.15)
		60	FR 2	0.95	0.47
		60	FR 5	0.75	0.15
		60	FR 10	1.74	0.14
		60	FR 20	0.48	0.00
M1	1	10	FR 1	0.92 (0.34)	0.92 (0.34)
		10	FR 2	1.13	0.56
		10	FR 5	0.51	0.09
		10	FR 10	1.51	0.14
		10	FR 20	0.99	0.04

		30	FR 1	0.50 (0.08)	0.50 (0.08)
		30	FR 2	0.36	0.18
		30	FR 5	0.85	0.14
		30	FR 10	0.46	0.04
		30	FR 20	0.68	0.00
		60	FR 1	0.26 (0.2)	0.24 (0.16)
		60	FR 2	0.20	0.10
		60	FR 5	0.55	0.11
		60	FR 10	0.67	0.04
		60	FR 20	0.20	0.00
M3	1	10	FR 1	1.80 (0.34)	1.80 (0.34)
		10	FR 2	2.33	1.17
		10	FR 5	0.54	0.08
		10	FR 10	1.27	0.13
		10	FR 20	0.76	0.00
		30	FR 1	1.07 (0.1)	1.07 (0.1)
		30	FR 2	0.75	0.38
		30	FR 5	1.02 (0.74)	0.19 (0.17)
		30	FR 10	0.85	0.09
		30	FR 20	1.45	0.04
		30	FR 40	0.76	0.00
		60	FR 1	1.51 (0.24)	1.46 (0.17)
		60	FR 2	1.14	0.57
		60	FR 5	1.36	0.27
		60	FR 10	1.03	0.09
		60	FR 20	0.60	0.00
BB	2	10	FR 1	1.67 (0.16)	1.67 (0.16)
		10	FR 2	2.19	1.08
		10	FR 5	3.51	0.69
		10	FR 10	2.97	0.30
		10	FR 20	3.73	0.19

		10	FR 40	2.08	0.05
		10	FR 80	1.50	0.02
		10	FR 160	0.86	0.00
		30	FR 1	1.90 (0.53)	1.90 (0.53)
		30	FR 2	2.72	1.36
		30	FR 5	2.35	0.47
		30	FR 10	2.89	0.28
		30	FR 20	2.94	0.15
		30	FR 40	2.11	0.04
		30	FR 80	2.00	0.02
		30	FR 160	0.64	0.00
		60	FR 1	2.17 (0.48)	2.16 (0.48)
		60	FR 2	2.91	1.44
		60	FR 5	3.17	0.62
		60	FR 10	3.36	0.32
		60	FR 20	2.45	0.12
		60	FR 40	1.44	0.04
		60	FR 80	1.98	0.02
		60	FR 160	0.96	0.00
PP	2	10	FR 1	1.06 (0.41)	1.05 (0.41)
		10	FR 2	2.23	1.11
		10	FR 5	2.52	0.50
		10	FR 10	1.70	0.16
		10	FR 20	0.83	0.03
		10	FR 40	0.86	0.02
		10	FR 80	0.67	0.01
		10	FR 160	0.52	0.00
		30	FR 1	1.26 (0.85)	1.26 (0.85)
		30	FR 2	1.96	0.96
		30	FR 5	1.18	0.24
		30	FR 10	0.82	0.08

30	FR 20	0.55	0.02
30	FR 40	0.77	0.02
30	FR 80	0.58	0.00
60	FR 1	1.07 (0.3)	1.06 (0.28)
60	FR 2	0.66	0.33
60	FR 5	0.59	0.11
60	FR 10	1.09	0.10
60	FR 20	0.56	0.03
60	FR 40	1.02	0.02
60	FR 80	0.85	0.01
60	FR 160	0.50	0.00